

MULTIENNIAL REPRODUCTION IN FEMALES OF A VIVIPAROUS,
TEMPERATE-ZONE SKINK, TILIQUA NIGROLUTEA

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Abstract: Reproductive frequency in captive and wild-caught female Tiliqua nigrolutea was examined over five consecutive reproductive seasons. Reproductive frequency (0.38 ± 0.035) was clearly different from an annual pattern of 1.0 (i.e. all females reproducing every year). Individual females did not reproduce every year, but “skipped” seasons were staggered such that a proportion of the population produced a clutch each season. Skipped reproductive opportunities are attributed to a combination of a long gestation, high relative clutch mass (0.43 ± 0.034), parturition late in the active season, a cessation of feeding in the latter stages of gestation and low autumn temperatures limiting post-partum feeding opportunities.

Keywords: Lizard; Multiennial cycle; Relative clutch mass; Reproductive frequency; Skink; Temperate-zone; Tiliqua nigrolutea, Viviparous

INTRODUCTION

Cool- and cold-temperate zone squamates are constrained by the need to reproduce during the warmer months of the year (Saint Girons, 1985; Shine, 1985) and parturition usually occurs at the time of year that provides optimal conditions for growth and survival of neonates (Abts, 1988; Callard et al., 1972; Goldberg, 1971; Olsson and Shine, 1997; 1998; Vitt and Lacher, 1981). In temperate regions, this is generally summer or early autumn (James and Shine, 1985; Jones and Swain, 1996; Jones et al., 1997; Naulleau and Fleury, 1990; Van Wyk, 1994; Whittier et al., 1987).

The timing of ovulation and the length of gestation are key variables determining when parturition occurs in viviparous squamates (Heatwole and Taylor, 1987; Wapstra et al., 1999), and are themselves determined, at least in part, by the length of the activity season. In most viviparous squamates, females are able to reproduce annually (Gavaud, 1983; Shine, 1985; Yokoyama and Yoshida, 1994), but if the active season is short, there may be insufficient time to complete vitellogenesis, ovulation, gestation and parturition in a single season (Olsson and Shine, 1999; 1998; Cree and Guillette, 1995; Saint Girons 1985). In such cases, females are unable to reproduce annually, and bi-, tri- or multiennial cycles are observed (Luiselli et al., 1996; Naulleau and Fleury, 1990; Olsson and Shine, 1999; Van Wyk, 1991).

Multiennial patterns of reproduction may be achieved in one of two ways: the reproductive cycle may be extended to span more than one active season, or a reproductive opportunity may be “skipped” in the year(s) following a reproductive effort. Lengthening of the reproductive cycle so that it extends over more than 12 months may be achieved in different ways. Extending vitellogenesis may prolong the ovarian cycle, as occurs in the viviparous biennially breeding lizards Barisia monticola (Vial and Stewart, 1985) and Hoplodactylus maculatus (Cree and Guillette,

1995), in which ovarian activity is effectively continuous. Gestation may be greatly extended by holding embryos over winter, as in Niveoscincus microlepidotus and Niveoscincus greeni (Hutchinson et al., 1989; Olsson and Shine, 1998). The lengthening of the cycle in either of these ways usually occurs in species living in cool- or cold-temperate regions (Cree and Guillette, 1995; Hutchinson et al., 1989).

Another strategy for achieving a multiennial cycle is exemplified by the viviparous lizard Liolaemus pictus. This species responds to short, cold activity seasons by assigning vitellogenesis and gestation to separate activity seasons with a period of gonadal latency during the intervening winter (Ibargüengoytia and Cussac, 1996). Several other viviparous squamate species, including the snakes Vipera berus (Prestt, 1971) and Vipera aspis (Naulleau and Fleury, 1990), and the lizards Anguis fragilis (Patterson, 1983) and Xantusia riversiana (Goldberg and Bezy, 1974), are reported to display multiennial reproductive cycles, but the mechanisms by which these are achieved is uncertain.

Alternatively, a reproductive effort may be completed within one active season, but the female may then “skip” one or more years before reproducing again. Such multiennial cycles occur in females of some temperate-zone reptile species that produce clutches of moderate to large size (Whittier and Crews, 1987), particularly in females of large, long-lived species (Bull and Shine, 1979; Whittier and Crews, 1987) and those which are viviparous (e.g. Cordylus giganteus (Van Wyk, 1991)) or egg-brooding (e.g. Eumeces okadae (Hasegawa, 1984)) (Bull and Shine, 1979). It has been suggested that females of some species exhibit greater lifetime reproductive success by “skipping” reproductive opportunities than by reproducing annually (Whittier and Crews, 1987; Whittier et al., 1987), because a greater proportion of their reserves can be devoted to growth in those seasons in which they do not produce a

clutch (Schwarzkopf, 1993) and SVL is often positively correlated with clutch size (Shine, 1980). However, it is difficult to measure lifetime reproductive success in long-lived species, particularly in the wild (Madsen and Shine, 1996), and there is a distinct lack of such linear studies, particularly in species that do not reproduce annually. We have studied a captive population of wild-caught blotched blue-tongued skinks, Tiliqua nigrolutea, over five consecutive reproductive seasons in Tasmania, Australia, at the cold extreme of its range. During this time we also gathered information on wild individuals.

Tiliqua nigrolutea is a large, viviparous skink with a cool-temperate zone distribution in south eastern Australia (Rawlinson, 1974). Males display a clear annual pattern of spermatogenesis, mating and quiescence (Edwards and Jones, in press a), but females display several life history characteristics suggestive of a multiennial pattern of reproduction. They exhibit a reproductive cycle that is completed within a single active season (Edwards, 1999), despite their cool-temperate zone distribution in Tasmania, Australia and the associated limited active season (late September – April). Gestation of the single clutch is long (approximately 4 – 4.5 months (Edwards and Jones, in press b; Shea, 1992)) by comparison with 3.5 - 4 months for sympatric viviparous species (Jones and Swain, 1996; Jones et al., 1997; Wapstra et al., 1999). Parturition in T. nigrolutea usually occurs late in the active season (Austral autumn: March - April). Females feed little, or not at all, during the final weeks of gestation, and cease feeding altogether in late autumn (late April - May), ahead of the start of the hibernation period (late May) (Edwards and Jones, in press b). A previous study, based solely on museum specimens of T. nigrolutea from throughout their range (Tasmania and south-eastern mainland Australia), suggested that females did not reproduce annually (Shea, 1992). Of 50 adult-sized specimens

examined, only 24 showed vitellogenic or ovulated follicles during the time when gravid females were present in the population (Shea, 1992). The present study aims to confirm the existence of a non-annual reproductive cycle in female T. nigrolutea in Tasmania using captive-, wild-mated and autopsied road-killed specimens, and to characterize the mechanism by which such a cycle is achieved.

MATERIALS AND METHODS

Female lizards were captured opportunistically by hand or collected as fresh road-killed specimens around Hobart (42°53'S, 147°19'E), Tasmania, Australia, during their active season. Captive animals were housed in roofed enclosures 1.9 x 3.4 x 2.1 m, which were wire-fronted allowing access to UV light and a natural photoperiod. Direct sunlight and a 120-W globe as an additional heat source suspended 30 cm above the floor at the front of each cage provided a thermal gradient across which the lizards could thermoregulate. Bark and leaf litter, in which the animals could hide, were also provided. Mixed-sex groups of approximately five animals were maintained in each cage, so that females could mate. Lizards were fed three times weekly during the active season (September – April). Their diet consisted of tinned catfood (meat varieties), snails when available, and a selection of fresh fruits, including apple and banana. Water was available ad libitum. Wild-mated individuals were held under the same conditions, but for much shorter periods of time, as these were caught after the mating period (November) in any given year. A colony of approximately 25 females and 15 males was maintained for the duration of the study, although individuals were held for a varying number of seasons determined by the requirements of a larger study into the reproductive physiology of the species (Edwards, 1999).

Female snout-vent length (SVL) ($\text{cm} \pm 0.1$) and mass ($\text{g} \pm 0.01$) at capture and/or regularly throughout gestation, female post-parturient mass, clutch mass and clutch number were all recorded. From intact road-killed individuals and several animals killed for parallel physiological experiments, total body and total gonadal mass were recorded and a gonadosomatic index (GSI) was calculated.

In a subset of captive females ($N = 8$) held for at least one quiescent season before a reproductive effort, SVL was recorded at the start (September) and finish (April) of both the quiescent and subsequent reproductive season, to compare female growth differences between reproductive conditions. Growth was recorded as:

$$(\text{SVL (end of season)} - \text{SVL (start of season)}) / \text{SVL (start of season)} * 100.$$

Reproductive frequency (RF) was examined over five consecutive reproductive seasons (1995/1996 – 1999/2000), both within each season in sub-samples of the wild population around Hobart, Tasmania, and over time in captive individuals. Females that had vitellogenic or ovulated follicles at autopsy or on palpation, or were observed to produce a clutch in autumn (March-April) were considered to be reproductively active in that year. The presence of corpora lutea (CLs) or corpora atretica (CAs) at autopsy were assumed to infer a recent reproductive effort. Non reproductive females were those in which ovaries were completely quiescent, containing only small ($< 5\text{mm}$), non-vitellogenic follicles, or those which did not produce a clutch. Reproductive frequency within each season was assessed in each of the five reproductive seasons of this study in a total of 112 individual adult females, by comparing the ratio of reproductively active and quiescent females. Reproductive frequency over time was calculated for each captive individual as:

$$\text{Total number of clutches produced} / \text{Number of seasons in captivity}.$$

Many females in the captive population ($N = 30$) were held for two or more consecutive reproductive seasons, so RF could be determined for these females individually. The population RF was assessed in each season for captive- and wild-mated individuals separately.

Relative clutch mass (RCM) was examined as a measure of female reproductive effort and was calculated for each parturition event as:

$$\frac{\text{Total neonate (live and stillborn) mass (g)}}{\text{Maternal post-partum mass (g)}}$$

This avoids the maternal mass occurring in both the numerator and the denominator (Shine, 1980). Females occasionally expelled a yolky, unfertilized egg during parturition; the mass of such eggs was not included in the calculation of clutch number or RCM. This calculation also excluded the mass of the amniotic fluid expelled at birth, and therefore represents a conservative estimate of female reproductive effort. At parturition a small amount of yolk remained in the embryonic yolk sac. This was immediately consumed by the neonate, and as it represents a maternal contribution towards her clutch and so a reproductive cost, the mass of this residual yolk was included in the total neonate mass used to calculate RCM.

All statistical analyses were performed using SYSTAT 7.0 for the PC (Wilkinson et al., 1998). A significance level of $\alpha = 0.05$ was used throughout. All data satisfied the assumptions of normality and homogeneity of variance. Chi squared analysis was used to assess whether the frequency of reproduction varied significantly from an annual pattern (i.e. all females reproduce every year) in captive- and in wild-mated females. Regression analysis was used to examine the relationship between female body size and both clutch number and RF over time. Analysis of variance (ANOVA) was used to examine the variation in both RCM and clutch number

between seasons. Unpaired Student's *t* tests examined the differences in RCM and clutch number between captive- versus wild-mated individuals over all seasons combined and a paired Student's *t* test was used to examine differences in growth between seasons. All values presented are means \pm one standard error (1 SE).

RESULTS

Yolked follicles were observed at autopsy only in spring, but not in all animals examined. In reproductively active females, vitellogenesis commenced at spring emergence (late September) and was completed relatively rapidly by late spring (mid-November). There was no indication of any yolk deposition in follicles during the post-partum period (April). The timing of the ovarian cycle is reflected by changes in the GSI (Fig. 1).

Adult female *T. nigrolutea* ranged from 26 - 31.5 cm SVL and weighed between 270 - 500 g, increasing to as much as 700-800 g during late gestation. A subset of females ($n = 8$) held for a quiescent followed by a reproductively active season demonstrated a greater mean percentage increase in SVL in the quiescent season (1.6 ± 0.58 %) than in the season in which a clutch was produced (0.6 ± 0.30 %), although this was not a significant difference ($t = 1.848$, $df = 7$, $P = 0.107$).

Mean RCM and mean clutch number in both captive- and in wild-mated females did not vary significantly between years for the five consecutive reproductive seasons of this study (1995/1996 - 1999/2000). Relative clutch mass also did not differ between mating states (captive versus wild) when data were combined across seasons. There was no significant difference in SVL or clutch number between captive- and wild-mated females over the five consecutive seasons of this study. Therefore, data were pooled to give a mean RCM for *T. nigrolutea* of 0.43 ± 0.034 (n

= 24). Mean clutch number was 8.3 ± 0.68 (range 2-15) and it was significantly correlated with maternal snout-vent length (SVL) ($y = 1.17x - 26.08$, $r^2 = 0.346$, $P = 0.003$) (Fig. 2).

When captive- and wild-mated individuals were considered separately by season, RF differed significantly from an annual pattern in several seasons in the captive (1996/1997, $\chi^2 = 13.00$, $df = 1$, $P < 0.005$) and wild (1995/1996, $\chi^2 = 8.47$, $df = 21$, $P < 0.005$; 1999/2000: $\chi^2 = 8.64$, $df = 1$, $P < 0.005$) populations (Table 1). However, in seasons which did not differ significantly from an annual pattern, not all females were reproductively active. There were no differences in clutch number, RCM or female SVL between captive- and wild-mated individuals within each season, so a combined data set is also included (Table 1). From the combined data, in three of the five seasons considered, RF differed significantly from an annual pattern of reproduction (1995/1996, $\chi^2 = 12.89$, $df = 1$, $P < 0.002$; 1996/1997, $\chi^2 = 15.04$, $df = 1$, $P < 0.0005$; 1999/2000, $\chi^2 = 10.71$, $df = 1$, $P < 0.0005$).

Mean RF over time ($n = 30$) was 0.38 ± 0.035 , which is clearly different from the frequency of 1.0 expected for an annual pattern of reproduction. Within this data set, some ($n = 11$) animals reproduced after one quiescent season, some ($n = 15$) after more than one skipped opportunity and some ($n = 4$) did not reproduce during the study (Table 2). In five successive seasons, only two individuals produced clutches in successive seasons. Regression analysis showed that RF over time was not related to female SVL ($y = 0.01x + 0.14$, $r^2 = 0.014$, $P = 0.666$).

DISCUSSION

Females of the blue-tongued skink, Tiliqua nigrolutea display a multiennial reproductive cycle in Tasmania, Australia. Females of this species are not strictly bi-

or triennial reproducers, but exhibit plasticity in RF, both between seasons and between individuals. This reproductive pattern is achieved by completing all phases of the reproductive cycle within a single active season, then skipping one or more reproductive opportunities in subsequent seasons.

This infrequent and irregular reproduction by females is unlikely to be a reflection of eggs or embryos being resorbed, either spontaneously in the wild or as a consequence of capture. There is, indeed, little evidence for embryo resorption in squamate reptiles (Blackburn, 1998). Captive female T. nigrolutea in this study were observed, on several (N = 4) occasions, to pass and consume large yolky masses (unfertilised ova) during parturition, implying that such masses are not resorbed during gestation. This phenomenon has been previously reported for Tiliqua scincoides (LeBreton, 1990), and we have observed unfertilised ova in the oviducts in pregnant female T. nigrolutea (N=3) at autopsy.

Vitellogenesis is initiated and completed over a relatively short time in the active season in T. nigrolutea (Fig. 1), as in the snake species Naja naja (Lance and Lofts, 1978), Nerodia sipedon (Aldridge, 1982), Tropidoclonion lineatum (Krohmer and Aldridge, 1985) and Trimeresurus flavoviridis (Yokoyama and Yoshida, 1994). This is in contrast to the strategy of commencing vitellogenesis in the post-partum period and completing it the following spring, utilised by several other viviparous squamates which are able to reproduce annually, such as Crotalus viridus (Aldridge, 1979), Pseudocordylus m. melanotus (Flemming, 1993). Similarly, two viviparous lizard species sympatric with T. nigrolutea, Niveoscincus metallicus (Jones and Swain, 1996) and Niveoscincus ocellatus (Wapstra et al., 1999; Jones et al., 1997), mate in autumn during mid-vitellogenesis and store sperm until spring ovulation (Jones et al., 1997; Swain and Jones, 1994; Wapstra et al., 1999). This allows

ovulation to occur earlier (September) than in T. nigrolutea (November), and gestation is slightly shorter, so that parturition occurs in mid-summer (January) (Jones et al., 1997; Swain and Jones, 1994).

In some species, late parturition and low autumn temperatures do not allow females time to store sufficient reserves both to endure winter hibernation and to become vitellogenic in the following spring (Saint Girons, 1985). Female T. nigrolutea noticeably reduced feeding during the latter stages of gestation. Although this phenomenon has not been quantified, it is likely to amplify the effects of a long gestation, high relative clutch mass, parturition late in the active season and low autumn temperatures limiting post-partum feeding on the ability to store fat reserves for future reproductive efforts. Some or all of these factors may regularly result in missed opportunities for reproduction (Saint Girons, 1985) as is reported, for example, in the lizards Eulamprus tympanum (Schwarzkopf, 1996), C. giganteus (Van Wyk, 1991) and A. fragilis (Patterson, 1983). A similar reduction in feeding during the latter stages of gestation has been demonstrated in several snake (Gregory et al., 1999; Macartney and Gregory, 1988) and lizard (Schwarzkopf, 1996) species, and may be due to limited space in the body cavity due to the presence of eggs or embryos (Schwarzkopf, 1996).

In some viviparous squamates, females display a plastic reproductive cycle in that they have the ability to breed annually if conditions (with respect to stored energy or warm thermal conditions) are good. In the snakes V. aspis, (Zuffi et al., 1999), E. longissima (Bonnet and Naulleau, 1994) and Thamnophis sirtalis parietalis (Whittier and Crews, 1990) and the lizard E. tympanum (Rohr, 1997), stored energy is the limiting factor in the regulation of reproduction; females do not become vitellogenic in a given year if their stored fat reserves are below a threshold level.

Reproductive frequency in captive- and wild-mated female T. nigrolutea in each season varied from 20.8 - 67.9%, suggesting an element of plasticity to their cycle, which would allow them to cope with the somewhat unpredictable climate of Tasmania. Given the variation in reproductive frequencies between individual females and the observation of two females reproducing in consecutive seasons, it seems possible that female T. nigrolutea could utilize this type of plasticity as a strategy for coping with the unpredictable climate in Tasmania, where the length and thermal quality of the active season are variable. In those years that the active season is relatively cool or short and post-partum feeding opportunities are limited, females are able to devote the following season to growth and storing reserves for future reproductive efforts, rather than production of a smaller clutch. Such a strategy has been reported in the lizard E. tympanum (Schwarzkopf, 1996; 1993) and the snake N. sipedon (Brown and Weatherhead, 1997). The data presented here do not strongly support the existence of this strategy in female T. nigrolutea, but sample size was small and several individuals had already attained near maximal recorded body size. While SVL in ectotherms does continue to increase throughout life, growth rate declines with age (Castanet et al., 1988; Chinsamy et al., 1995; Montori, 1990). This may explain the lack of a significant difference between growth in quiescent and reproductive seasons in this study.

Reproductive frequency in captive-mated female T. nigrolutea in each season varied significantly from an annual pattern in only a single season. This is likely to be an artifact, as other aspects of a physiological study on the captive population resulted in post-partum females being released to maximize space for potentially reproductively active females in an attempt to characterize cycles of steroid hormones throughout reproduction (Edwards and Jones, in press b). However, the linear study

clearly demonstrates that individuals generally do not reproduce every year, and there may be one, two or even three seasons between reproductive efforts, as has been reported for the viviparous snakes V. berus (Prestt, 1971), V. aspis and Elaphe longissima (Bonnet and Naulleau, 1994) and the lizards E. tympanum (Schwarzkopf, 1993) and C. giganteus (Van Wyk, 1991).

A mean RCM of 0.43 ± 0.034 for female T. nigrolutea over the five seasons of this study suggests that the effort of reproduction is high. This mean RCM is comparable with those of other viviparous squamates that are regarded as having a high RCM (0.52 in Lerista bougainvillii (Qualls and Shine, 1995) and 0.482 in Aspidelaps scutatus (Shine et al., 1996)). It is also well above the RCM of two sympatric, annually reproducing viviparous skinks, N. metallicus (0.307) (C. McCoull, personal communication) and N. ocellatus (0.230 (in 1995/1996) and 0.290 (in 1996/1997)) (Wapstra and Swain, in press). The mean RCM for T. nigrolutea reported in this study is also very similar to the RCM of 0.4 reported for Tiliqua rugosa, (Fergusson and Algar, 1986), although these authors did not provide details of the calculation used. Thus, although T. nigrolutea does not reproduce annually, once the commitment to produce a clutch is made, a large reproductive effort is allocated, perhaps offsetting the cost to life-time fecundity of not producing a clutch each year.

Tasmania represents the southernmost part of the range of T. nigrolutea, in which any effects of the cool environment and limited active season are likely to be amplified, although a study using museum specimens indicated that female T. nigrolutea on the Australian mainland are also likely to be non-annual breeders (Shea, 1992). However, no measures of RF or RCM have been reported for any mainland populations of this species. Other members of the genus with more northerly ranges usually reproduce annually (Shea, 1992). It is likely that the multiennial cycle of

female T. nigrolutea reflects a combination of high RCM and limited thermal opportunities (short active season).

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Table 1 Reproductive frequency of captive- and wild-mated female Tiliqua nigrolutea in each of five reproductive seasons from 1995 – 2000, NS = not significantly different from an annual pattern of reproduction.

Where mated	1995/1996	1996/1997	1997/1998	1998/1999	1999/2000
Captivity (n)	11	13	19	9	7
(% Reproductive)	57.1	0	57.9	55.5	28.6
	NS	$\underline{P} < 0.0005$	NS	NS	NS
Wild (n)	17	11	9	6	14
(% Reproductive)	71.4	45.5	88.9	50.0	21.4
	$\underline{P} < 0.0005$	NS	NS	NS	$\underline{P} < 0.005$
Combined (N)	28	24	28	15	21
(% Reproductive)	37.5	20.8	67.9	53.3	23.8
	$\underline{P} < 0.002$	$\underline{P} < 0.0005$	NS	NS	$\underline{P} < 0.0005$

Table 2 Reproductive frequency, number of seasons in captivity and number of clutches produced by captive individuals (n = 30) held for two or more consecutive seasons between 1995 and 2000.

Reproductive frequency	Captive seasons	Reproductive events	n
0.67	3	2	3
0.5	2	1	11
0.4	5	2	2
0.34	3	1	6
0.25	4	1	3
0.2	5	1	1
0	2-5	0	4

FIGURE LEGENDS

Figure 1 Gonadosomatic index for female Tiliqua nigrolutea showing the vitellogenic period confined to spring. Hibernation (n = 2), Early vitellogenesis (n = 3), Late vitellogenesis (n = 4), Gestation (n = 3), Post-parturition (n = 4). Values are means and standard errors are not included due to small sample sizes.

Figure 2 Relationship between female snout-vent length and number of offspring (n = 24). The equation for the linear regression is: $y = 1.17x - 26.09$, $r^2 = 0.346$, $P = 0.003$.

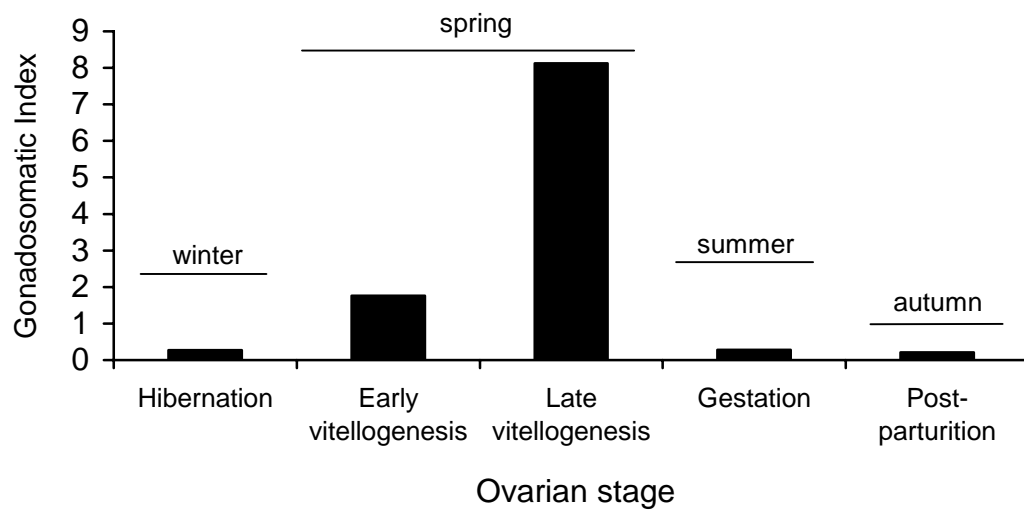


Figure 1

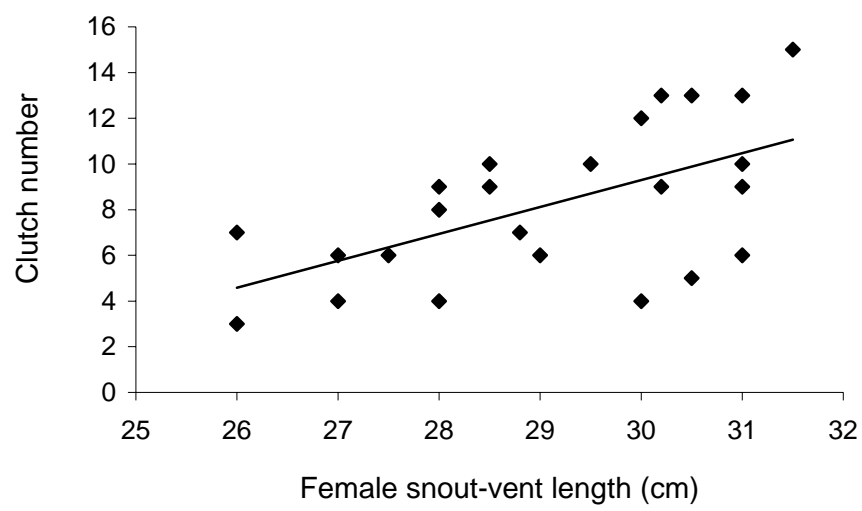


Figure 2